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Mapping local and regional distribution of *Lygophis paucidens* Hoge, 1952 (Serpentes, Dipsadidae), an elusive snake from the sandy savannas of Brazil and Paraguay

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Abstract

Lygophis paucidens Hoge, 1952 is a rare Neotropical snake, previously mapped using only a few individuals in five localities. Herein we update and discuss the distribution and conservation status of *L. paucidens* within major Neotropical ecoregions, providing previously unavailable data on distribution and habitat use. We compiled and mapped point locality records from literature and museum specimens, complemented by field studies in three localities. We used those records to map the species Extent of Occurrence (EOO) and Area of Occupancy (AOO), two range-related metrics of central relevance for conservation. We recovered 52 records from 46 vouchered specimens and six field records, distributed in 35 individual point localities, all within the diagonal of open vegetation in South America, with most records in cerrado savannas with sandy soils. *Lygophis paucidens* is likely a psammophilous species, which might explain its occurrence in savanna enclaves in forested ecoregions and its potentially discontinuous distribution. This knowledge is, therefore, useful in aiding future conservation assessments.

Keywords

Biogeography, Cerrado, conservation, open grasslands, sandy soils, savanna, Xenodontinae.

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Introduction

The Neotropical snake genus *Lygophis* Fitzinger, 1943 is distributed throughout South America, from Venezuela to Argentina and mostly associated with open areas of the Guyana shield or with savannas and drylands in the diagonal of open vegetation in South America (Dixon 1989). This genus belongs to the tribe Xenodontini in the family Dipsadidae, the richest snake family in the Neotropical region (Grazziotin et al. 2012; Uetz et al. 2019). The genus *Lygophis* was recently resurrected by Zaher et al. (2009). It was supported as a distinct monophyletic group (Grazziotin et al. 2012; but see Curcio et al. 2009) and is comprised of eight species (Uetz et al. 2019).

Lygophis paucidens Hoge, 1952 is an elusive snake described from a specimen from Mato Verde, state of

Mato Grosso, central Brazil. Since then, the most recent available map of its distribution was provided by Dixon (1989), using only five point localities. This species has not yet been assessed by the International Union for Conservation of Nature (IUCN 2019), and it is not included in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) appendices (CITES 2017), although it is considered as "Least Concern" (LC) in the Brazilian List of Threatened Species of Fauna (Machado et al. 2008; ICMBIO 2018). Due to the low numbers of specimens, information on its natural history is still scarce. It preys mostly lizards of the family Teiidae (Hoge 1952; Dixon 1989) such as *Ameivula* cf. *ocellifera* Spix, 1825 (Michaud and Dixon 1989). *Lygophis paucidens* is oviparous, diurnal, and terrestrial, actively hunting on the ground and occasionally found sheltered in leaf litter or under hollow logs (Pavan 2007; Rodrigues and Prudente 2011). Although *L. paucidens* is reported to occur only in open cerrado grasslands (Nogueira 2001), knowledge on its range and biogeographical aspects (such as elevation and ecoregions) are hampered by the lack of an updated map. Herein, we review the available reported localities and field records of *L. paucidens* and comment on its patterns of local and regional geographic distribution and conservation.

Methods

We reviewed deposited specimens at three herpetological collections in Brazil (**CHUNB,** Coleção Herpetológica of Universidade de Brasília; **IBSP**, Instituto Butantan; **MZUSP**, Museu de Zoologia da Universidade de São Paulo) (Table 1). Specimens were identified as *L. paucidens* by counting the number of maxillary teeth and ventral scales, coupled with a general analysis of colour pattern. We then compiled and reviewed the reported localities from the analysed vouchers and literature, and mapped them according to Brazilian biomes (IBGE 2019) and ecoregions outside Brazil (Dinerstein et al. 2017), and elevation using QGIS 3.4 (QGIS 2019). When exact coordinates were not available, we assigned records to the corresponding municipality using available online gazetteers (SpeciesLink 2019). Duplicate or uncertain records were not used. We also used additional data on field samples in three Cerrado localities (fieldwork data available in Nogueira 2001; Valdujo et al. 2009; Recoder et al. 2011) to provide data on activity and habitat use.

To further understand the distribution of *L. paucidens*, we used IUCN guidelines (IUCN 2019) and calculated EOO (extent of occurrence) and AOO (area of occupancy). EOO measures the general spatial range of a taxon, whereas AOO measures how much taxon-specific habitat is available and currently occupied by the taxon (IUCN Standards and Petitions Committee 2019). These metrics are analogous to the biogeographical scales proposed by de Candolle (1820): regional–station (EOO) and local–habitation (AOO). EOO was calculated using a minimum convex hull. For the more complex and data dependent AOO we analysed two contrasting and extreme scenarios: the first was obtained using only the available presence records; the second was obtained by mapping all areas with potential available habitat within the EOO polygon. In both cases (verified presence of potential presence in all areas of available habitat) we intersected point data with a 2 × 2 km grid cells (IUCN Standards and Petitions Committee 2019). To calculate available habitat we intersected these two layers: a land-use raster for remaining savanna patches in Cerrado (INPE 2013) and Caatinga (MMA 2011), as well as a soil type raster (Hengl et al. 2017), using areas with at least 60.5% of sand (the median value of % of sand in the soil of known presence records, see Results below). Both EOO and AOO were calculated using the GeoCAT Red List threat assessment support tool (Bachman et al. 2011).

Results

***Lygophis paucidens* Hoge, 1952**
Figure 1A, B

Material examined. Table 1.

Identification. *Lygophis paucidens* has a conspicuous pattern with three longitudinal dark lines on the back of the head (Fig. 1A. B), which quickly fade towards midbody. The hemipenis is clavate, with reduced lobes, reduced or absent interlobular sulcus and dorsal scale micro-ornamentation fasciculate (Moura-Leite 2001). It can be differentiated from other *Lygophis* species, such as *L. flavifrenatus* Cope, 1862, by the number of maxillary teeth (fewer than 13 in *L. paucidens*) and by its small optic foramen (Dixon 1989). Regarding pholidosis, *L. paucidens* presents the following counts: eight supralabials, 165–174 ventrals, 62–72 subcaudals, and 17-17-15 dorsal scale rows (Dixon 1989; Lema 1989; Cacciali et al. 2013).

Distribution. We compiled, reviewed, and mapped 35 point localities referring to 52 specimens of *L. paucidens* (Fig, 2), of which 46 were vouchered. Our map, thus, added 30 localities from the available literature and museum specimens to the point localities previously reported by Dixon (1989). This species was found to be widely distributed throughout several states from central and northeastern Brazil (Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pernambuco, Piauí, and Tocantins) and in the San Pedro Department in eastern Paraguay (Table 1). Most point localities are within open and dry ecoregions, mostly within cerrado savannas (83.3%), with isolated records in semi-arid Caatinga. The two points outside these ecoregions are in transition zones with Atlantic Forest and Amazonia (Fig. 2).

Table 1. Locality records for *Lygophis paucidens*. Collection codes for voucher numbers: CHNUB = Coleção Herpetológica da Universidade de Brasília; CHNUFPI = Coleção Herpetológica da Universidade Federal do Piauí; CZPLT = Para La Tierra Zoological Collection; CZDP = Coleção Zoológica Delta do Parnaíba; IBSP = Instituto Butantan; MNRJ = Museu Nacional, Rio de Janeiro; MPEG = Museu Paraense Emílio Goeldi; MZUFBA = Museu de Zoologia da Universidade Federal da Bahia; MZUSP = Museu de Zoologia da Universidade de São Paulo; UFMT = Universidade Federal de Mato Grosso; URCA = Universidade Regional do Cariri. Source: 1 = field collected; 2 = literature; 3 = analysed specimens.

Voucher	Country	Locality	State	Latitude	Longitude	Collected in	Source	Reference
IBSP50343	Brazil	Alto Paraíso	GO	−14.08	−047.62	—	1, 3	
MPEG17226	Brazil	Amarante do Maranhão	MA	−05.57	−046.74	1986	2	Prudente et al. 2018
CHUNB37262	Brazil	Arinos	MG	−15.91	−046.12	—	3	
MZUSP	Brazil	EE Uruçuí-Una, Baixa Grande do Ribeiro	PI	−08.88	−044.97	2000/2001	2	Dal Vecchio et al. 2013
CHUNB24448	Brazil	Núcleo Bandeirante, Brasília	DF	−15.78	−047.93	2001	1, 3	Nogueira 2001
MPEG22791, 22802	Brazil	Castelo do Piauí	PI	−05.32	−041.55	2005–2007	2	Rodrigues and Prudente 2011
CHUNB3771, UFMT675	Brazil	Chapada dos Guimarães	MT	−15.43	−055.75	—	2, 3	
CHUNB31335	Brazil	Cocalzinho	GO	−15.78	−048.77	—	3	
UFMT2347	Brazil	Cuiabá	MT	−15.58	−056.08	—	2	
MZUSP9597	Brazil	Gentio do Ouro	BA	−11.43	−042.50	—	2, 3	Guedes 2012
MZUSP12702	Brazil	Guaraí	TO	−08.83	−048.50	—	2, 3	
IBSP10448 - Paratype	Brazil	Ipameri	GO	−17.72	−048.16	1943	2	Hoge 1952
MNRJ 18656	Brazil	Jaborandi	BA	−13.62	−044.43	—	2	Guedes 2012
UFMT34	Brazil	Jangada	MT	−15.33	−056.55	—	2	
MNRJ15253	Brazil	Mateiros	TO	−10.74	−046.79		2	
IBSP12016 - Holotype	Brazil	Mato Verde, Luciara	MT	−11.22	−050.67	1948	2	Hoge 1952
CHUNB29666, MZUSP11106	Brazil	Niquelândia	GO	−14.05	−048.32	—	3	
CHUNB22070, IBSP64567, 65360, 65979	Brazil	Palmas	TO	−10.30	−048.35	—	3	
MZUSP14390	Brazil	Paranã	TO	−12.57	−047.88	2000	2	Pavan 2008
CZDP	Brazil	Ilha de Santa Isabel, Parnaiba	PI	−02.90	−041.78	—	2	Pereira and Guzzi 2015
CHUNB61141-44	Brazil	PN Sete Cidades, Piracuruca	PI	−04.11	−041.71	2010	1, 3	
MZUFBA1846, 1855	Brazil	Poções	BA	−14.54	−040.38	—	2	Guedes 2012
IBSP12832, IBSP12843 - Paratypes	Brazil	Rio São Domingos, Cocalinho	MT	−13.65	−051.15	1949	2	Hoge 1952
CZPLT-H122, H144	Paraguay	Laguna Blanca, San Pedro	San Pedro	−23.8	−056.29	2011	2	Cacciali et al. 2013
MZUSP10797	Brazil	Santa Rita do Araguaia	GO	−17.32	−053.20	—	3	
IBSP19959-60	Brazil	São Félix do Araguaia	MT	−11.62	−050.67	—	3	
IBSP51723	Brazil	São Francisco	MG	−15.95	−044.87	—	3	
IBSP1225-27 - Paratypes	Brazil	Teresina	PI	−05.08	−042.80	1917	2	Hoge 1952
CHNUFPI33	Brazil	Timon	MA	−05.36	−042.85	2005–2006	2	Silva et al. 2016
URCA-H5706	Brazil	Trairi	CE	−03.28	−039.27	2005–2013	2	Roberto and Loebmann 2016
CHUNB11558, 35356	Brazil	São Domingos	GO	−13.55	−046.35	—	3	
—	Brazil	José de Freitas	PI	−04.65	−042.35	2008	2	Cavalcante 2009
—	Brazil	Guarai	TO	−08.62	−048.32	2001	2	Pavan 2008
IBSP62696	Brazil	Assentamento Nascentes do Araguaia, Mineiros	GO	−17.67	−053.22	2000	1, 3	
MZUSP12874	Brazil	PN Grande Sertão Veredas, Formoso	MG	−15.25	−045.89	2001	1, 3	
—	Brazil	EE Serra Geral Tocantins, Mateiros	TO	−10.64	−046.65	2003	1	
—	Brazil	EE Serra Geral Tocantins, Mateiros	TO	−10.60	−046.81	2003	1	
—	Brazil	EE Serra Geral Tocantins, Mateiros	TO	−10.74	−046.79	2003	1	

Habitat. *Lygophis paucidens* was found in three Cerrado localities: Emas National Park and surroundings, Mineiros, Goiás state; Grande Sertão Veredas National Park, Formoso, Minas Gerais state; and Serra Geral do Tocantins Ecological Station, Mateiros, Tocantins state. All specimens were active during the day in sandy soil cerrado savannas, such as campo sujo, campo cerrado or campo limpo formations (Fig. 1C). In the literature, this species was reported to occur on open cerrado (n = 5), forested cerrado (n = 2), palm marshes (n = 2), semi-open cerrado (n = 1), and coastal vegetation (n = 1) (Pavan 2007; Rodrigues and Prudente 2011; Cacciali et al. 2013; Dal Vecchio 2013; Roberto and Loebmann 2016; Silva et al. 2016). The median percentage of sand in the soil for the mapped localities was 60.5%. Moreover, *L. paucidens* is distributed over a broad altitudinal range, occurring from sea level to over 1200 m (Fig. 2B).

Conservation. Even though the estimated EOO of *L. paucidens* was wide, with over 2 million km^2 (2,300,322 km^2), AOO calculated from the 2 × 2 grid cells was much lower with only 148 km^2 (not mapped due to its small area). On the other hand, AOO calculated using the intersection of sand-rich soil areas (over 60.5 %, the median

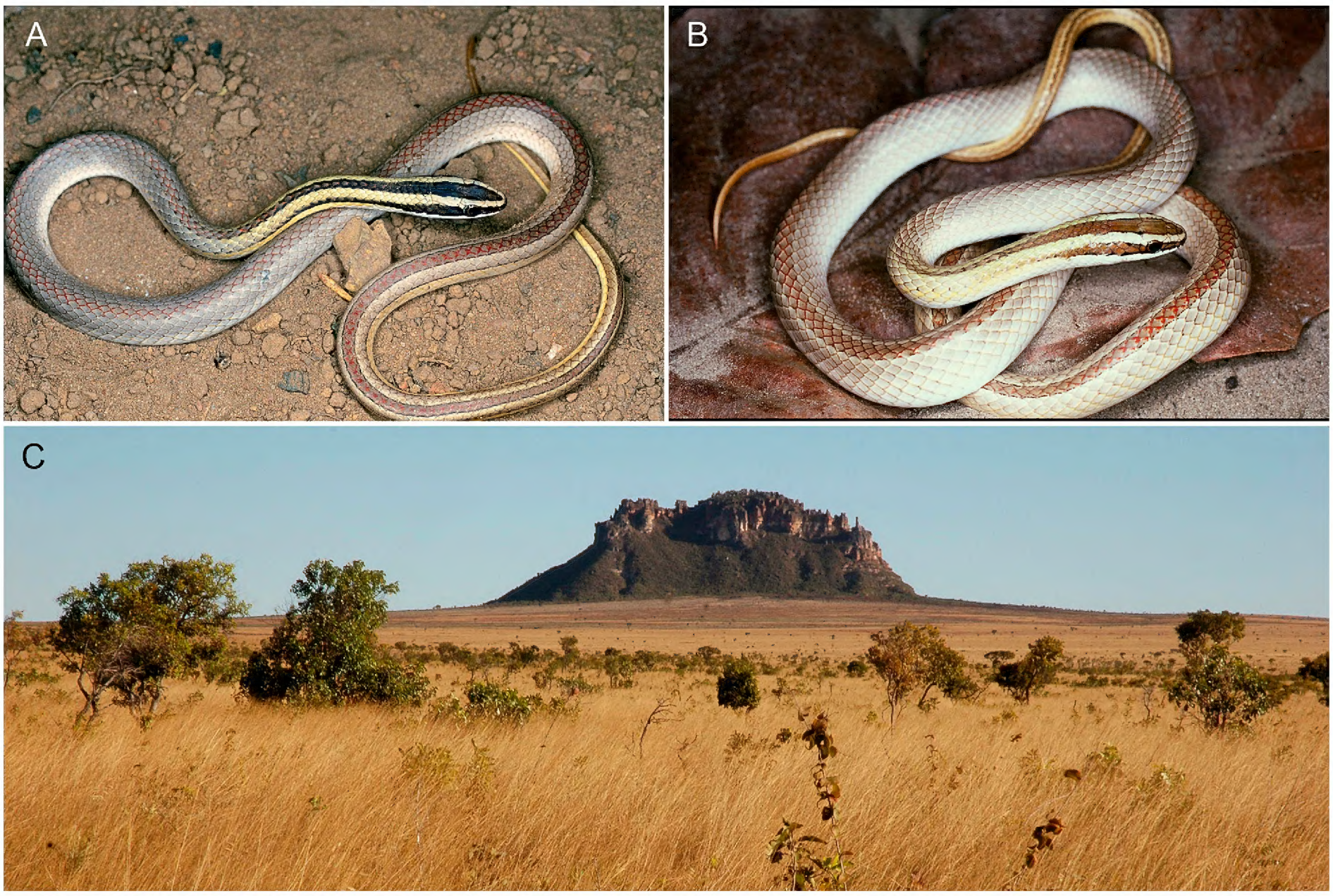

Figure 1. *Lygophis paucidens*. **A.** *Lygophis paucidens* from Mineiros, GO, Brazil. **B.** *Lygophis paucidens* from Parque Nacional Grande Sertão Veredas, Formoso, MG, Brazil. **C.** Typical habitat (Serra Geral do Tocantins Ecological Station, TO, Brazil). Photos by Cristiano de Campos Nogueira.

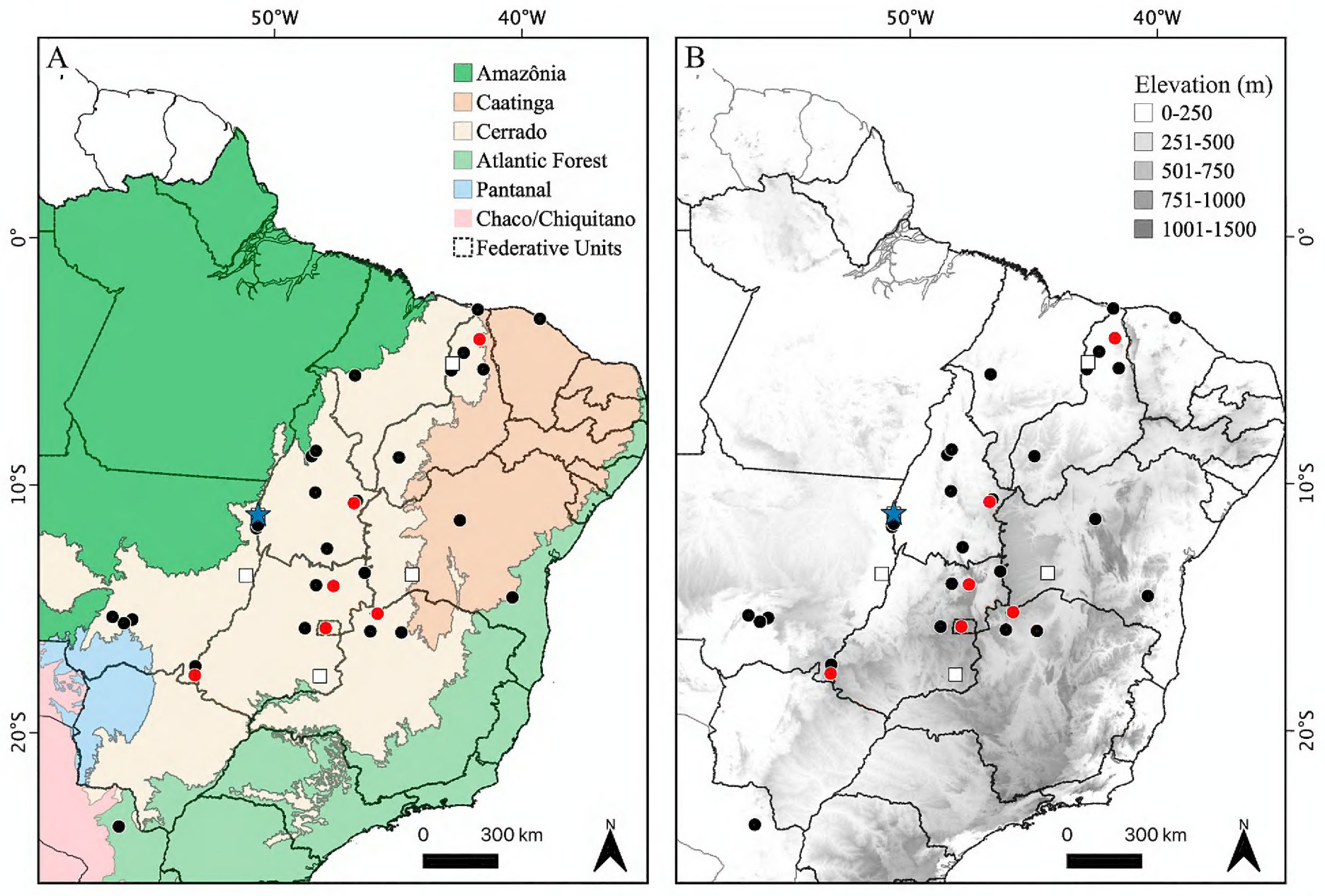

Figure 2. Geographical distribution of *Lygophis paucidens*. Map of distribution with **A.** ecoregions (adapted from IBGE 2019 and Dinerstein 2017) and **B**. elevation in South America. Localities previously mapped in Dixon (1989) are represented by white squares, of which ★ (blue star) denotes type locality. Circles represent localities previously not compiled and mapped: red circles represent field-confirmed records and black circles represent literature or museum records.

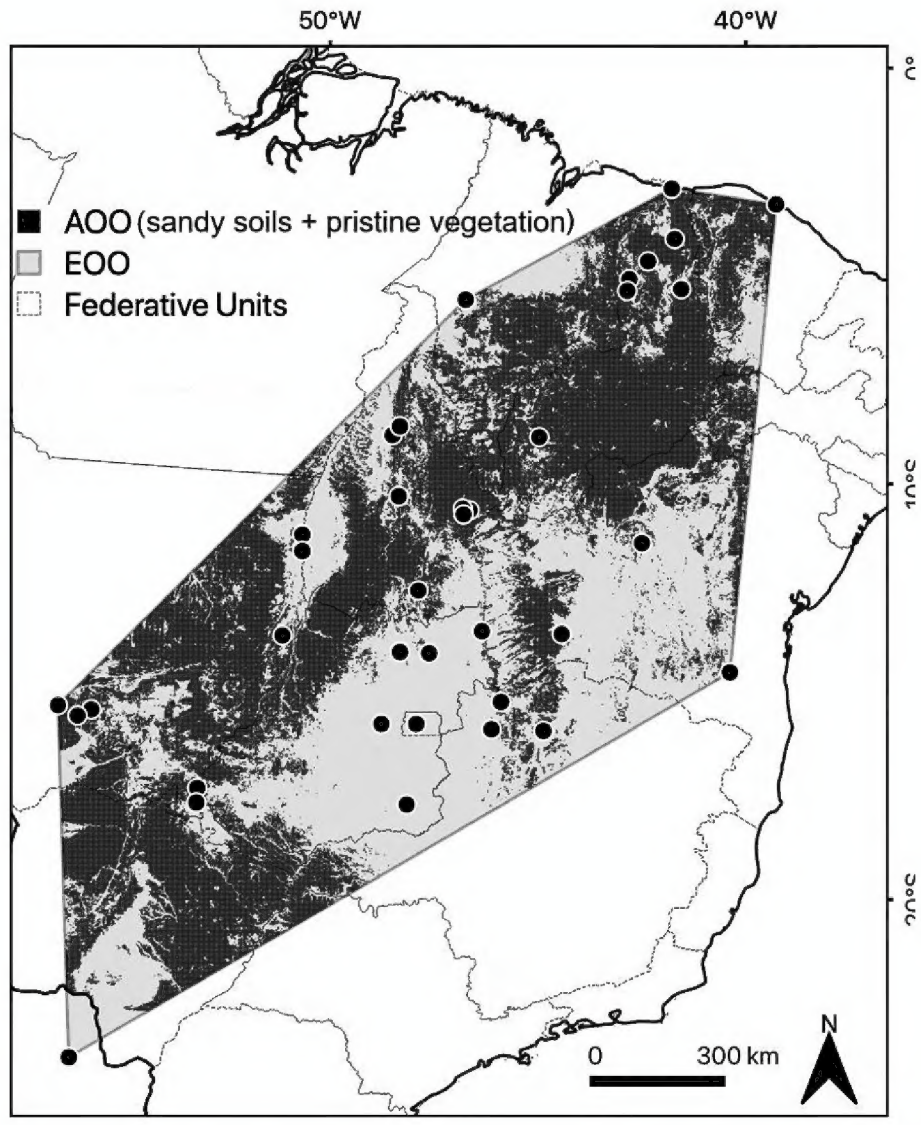

Figure 3. EOO (Extent of occurrence = 2,300,322 km²) and upper bound of AOO (Area of occupancy = 946,176 km²) of *Lygophis paucidens*. The upper bound of AOO is the total summed area of 2 × 2 km grid cells of remaining savanna patches on sandy soils in EOO.

value of % sand in the soil for reported localities) and remaining savanna areas in Cerrado and Caatinga was nearly 1 million km² (946,176 km²) (Fig. 3).

Discussion

Lygophis paucidens was previously considered as endemic to the Cerrado, being restricted to central Brazilian savannas (Nogueira et al. 2010, 2011). Our new maps and new data reveal its presence outside the Cerrado ecoregion. However, most records are still within this ecoregion, or at least close to its contact areas, especially with Caatinga (e.g. Bahia: Gentio de Ouro and Jaborandi; Piauí: Parnaíba and Teresina). However, in large scale ecoregion maps these relatively small and isolated patches of savannas are not visible and mapped, due to a problem of scale. Thus, the presence outside the Cerrado core region may simply reflect this shortcoming of large scale ecoregion maps that fail to capture local habitat variation and, thus, may obscure detailed distribution and endemism patterns. We caution that the detection of ecoregion endemics must always take into consideration that boundaries between major vegetation units must be taken with care, as contact areas between ecoregions are much more complex than linear boundaries suggest. Thus, we hypothesize that the presence of *L. paucidens* outside the main limits of the Cerrado is associated with small Cerrado enclaves within other vegetation zones, which are impossible to map at the continental scale. As a clear example, the record in Paraguay, far outside the Cerrado limits, is reported from a typical open, cerrado area on sandy soils (Laguna Blanca; Atkinson et al. 2008). Moreover, Sete Cidades National Park (Piracuruca), mapped in the Caatinga region, is actually dominated by typical cerrado savannas with sandy soils (Castro et al. 2010).

Until 2001, *L. paucidens* had only been reported for six localities (Nogueira 2001), but recent reports have considerably extended its range, including the single locality outside Brazil, a cerrado area in Reserva Natural Laguna Blanca (Paraguay), which extended this species' distribution by more than 700 km southwest from the nearest record (although reported erroneously as 320 km by Cacciali et al. 2013). It is unclear whether *L. paucidens* occurs continuously, since there are noticeable gaps in its distribution. These gaps are especially evident within the Brazilian Cerrado and in relatively well-sampled localities (e.g. Emas National Park), where it was only found outside the park, in sandy soil savannas near the Araguaia headwaters, but not inside the park, dominated by tabletop plateau savannas with clay-rich soils (Valdujo et al. 2013). This species, thus, seems to occur mainly on patches of sandy soils (Cacciali et al. 2013; this work), which suggests a discontinuous distribution across central Brazil, or at least rarified distribution outside areas dominated by sandy soils. We argue that this strong psammophilous association might explain its rarity and disjunct distribution and support its existence in patchy open habitat enclaves in other ecoregions (Guedes 2012), such as transition zones with Caatinga, Atlantic Forest, and Amazonia. This same distribution pattern and association with sandy soils is shared with other snake species such as *Bothrops lutzi* (Recoder et al. 2011) and *Psomophis joberti* (Nogueira et al. 2011).

Our study highlights the need to couple regional distribution and natural history data on local distribution to properly assess habitat, as proposed by early biogeographers such as de Candolle (1820). These two scales of study are complementary, and we can only understand ranges by adding detailed local scale information (as proposed by Wallace 1854) to large-scale mapping and revision of museum records, which might help to assess species conservation status. For *L. paucidens* the difference between the estimated lower and upper values of estimated AOO is remarkable. Using only known presence records (lower bound, see IUCN 2019) leads to classifying the species as "Endangered" , EN. On the other hand, using the much higher AOO estimated using all potential habitats, would classify the species as "Least Concern". These two extremes should be documented but avoided (see IUCN 2019), and new detailed mapping methods, coupled by expert opinion on range limits, could provide a more realistic estimate of AOO and a better assessment of threat, based on intermediate AOO values. This extreme variation in estimated AOO may be common in species with wide but discontinuous and complex ranges, and represents a challenge for biogeography and conservation assessments (e.g. see

Cardoso et al. 2012; Maes et al. 2015). Species with relatively wide ranges, but with localized habitats and rarified ranges may be overlooked in threat assessments due to their large EOO values, and the wide potential variations in AOO.

We hypothesize that further studies on other localities with sandy soils—especially inside the EOO—may reveal additional records of this species, including sandy savanna enclaves outside the core Cerrado area in Brazil. Those records outside the Cerrado core area may reflect the presence of localized patches of savannas on sandy soils, indicating relictual savannas not may not visible in continental scale maps (Furley 1999). Moreover, we suggest that the range of *L. paucidens* is naturally discontinuous, given its strong association to a specific discontinuous habitat type: savannas with sandy soils. Finally, we suggest analysing in detail life-history aspects of species with scarce information (e.g. habitat preference), which can help to connect local and regional patterns of their distribution (de Candolle 1820; Blondel 1987), and aid in understanding relictual or disjunct ranges of other similarly distributed taxa.

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Authors' Contributions

FS, JPSVA and JCD prepared the map and reviewed the available literature. CCN analysed the museum specimens and contributed with field records. FS, JPSVA, and JCD wrote the manuscript, with several precious contributions and suggestions by CCN.

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